

New host and distributional records for *Camarosporidiella* in Italy, Russia, and Ukraine

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ABSTRACT—*Camarosporidiella* specimens collected from woody plants in central Italy, eastern Ukraine, and southeastern Russia were identified based on morphology and multi-gene (LSU, SSU, ITS, and TEF) sequence analyses. *Camarosporidiella caraganicola* on *Amorpha fruticosa*, *C. celtidis* on *Ulmus pumila*, *C. elaeagnicola* on *Cytisus ruthenicus* are described with new host records and as new fungal records for Ukraine. *Camarosporidiella moricola* on *Morus nigra* is newly reported for Italy, and *C. robiniicola* on *Robinia pseudoacacia* is new for Ukraine. *Camarosporidiella elaeagnicola* on *Elaeagnus angustifolia* is re-described to facilitate identification. Notes on host distribution of *Camarosporidiellaceae* are also provided.

KEY WORDS—asexual, multigene, phylogeny, taxa, taxonomy

Introduction

The monotypic family *Camarosporidiellaceae* was introduced by Wanasinghe & al. (2017) for *Camarosporidiella* as type genus. *Camarosporidiella* species, which are necrotrophic or saprobic on host plants (Tibpromma & al. 2017, Wanasinghe & al. 2017), are mainly distributed in southern (Italy) and eastern Europe (Russia), central Asia (Uzbekistan), and Southeast Asia (Thailand) (Wanasinghe & al. 2017). There are 23 *Camarosporidiella* records listed in Index Fungorum (2020, accessed 2 August). Understanding species relationships within *Camarosporidiella* is complicated due to the lack of morphological characters available to distinguish species. Most species are characterized by asexual morphs producing conidia that are muriform, ellipsoidal, or fusiform and dark brown (Wanasinghe & al. 2017). Species exhibiting a sexual morph are characterized by globose to subglobose ascomata, cylindrical short-pedicellate asci, and ellipsoidal muriform ascospores. Accurate new host-fungus records are essential for identification and prevention of plant diseases (Dugan & al. 2018). New fungal reports facilitate deposition of new voucher specimens, contribute new molecular data in GenBank, expand knowledge surrounding host-specificity, and note new host-fungi interactions (Halme & al. 2012). In this study, we describe and illustrate six *Camarosporidiella* species and analyze DNA sequences that may facilitate their species identification. *Camarosporidiella caraganicola*, *C. celtidis*, *C. elaeagnicola* have new host records for Ukraine, and *C. moricola* on *Morus nigra* (in Italy) and *C. robiniicola* (in Ukraine) represent new distributional records. *Camarosporidiella elaeagnicola* on *Elaeagnus angustifolia* is re-described to enable identification. Host distributions of all six species are also discussed.

Materials & methods

Sample collection, morphological examination, and isolation

Fresh specimens were collected from southern European Russia (Rostov region), eastern Ukraine (Donetsk region), and central Italy (Forlì-Cesena province). No endangered or protected species were sampled. Twigs, branches, and stems were examined for fruiting bodies in the laboratory using a Motic SMZ 168 stereomicroscope. Single spore cultures were established according to Chomnunti & al. (2014). Conidia and ascospores were lifted from fruiting bodies using a sterile inoculation needle and dropped onto surfaces of malt extract agar (MEA) plates that were kept in a dry place overnight. Plates were checked using the stereomicroscope, and single germinated conidia or ascospores were transferred to new MEA plates. The culture media were kept at 25°C for 10 days (Damm & al. 2009). MEA colony morphologies (including colour, shape, and growth rate) were determined after 7 days of incubation. Microscopic fungal structures were mounted in water and observed using a Nikon Eclipse 80i compound microscope and photographed with a Canon 750D digital camera fitted to the microscope.

Voucher specimens are deposited in the Herbarium of Mae Fah Luang University, Chiang Rai, Thailand (MFLU). Single-spore cultures were preserved on MEA in 1.5 mL microtube slants at 4°C in Mae Fah Luang Culture Collection, Chiang Rai, Thailand (MFLUCC) with duplicates at Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures, Braunschweig, Germany (DSM). Tarosoft (R) Image Frame Work was used to measure sizes of microstructure, and Adobe Photoshop CS6 Extended (v. 10.0) was used to prepare photographic plates.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from scraped fresh fungal mycelium grown on MEA media for 8 weeks at 25°C by using the E.Z.N.A Fungal DNA Mini Kit (D3390-02) extraction kit following the manufacturer's protocol. Four regions [3'-end of 18S + ITS1 + 5.8S rRNA gene + ITS2 + 5'-end of the 28S rRNA gene; 28S rDNA gene (LSU); 18S rDNA gene (SSU); partial translation elongation factor 1-alpha gene (TEF)] were amplified and sequenced using the primer pairs ITS5 and ITS4 (White & al. 1990), LR0R (Rehner & Samuels 1994) and LR5 (Vilgalys & Hester 1990), NS1 and NS4 (White & al. 1990), and TEF1-983F and TEF1-2218R (Rehner & Buckley 2005). Polymerase chain reaction (PCR) mixtures and conditions for ITS, LSU, SSU, and TEF were amplified in 25-µL volumes according to Wanasinghe & al. (2017). Final mixtures comprised 1 µL genomic DNA extract, 12.5 µL of 2× Power Taq PCR MasterMix and 9.5 µL deionised water and 1 µL of each primer (10 µM). For each gene, PCR conditions included initial denaturation at 95°C for 5 min, 35 denaturation cycles at 95°C for 90 s, annealing for 90 s, elongation at 72°C for 1 min, and final extension at 72°C for 10 min. Annealing temperatures were 56°C for ITS and LSU, 55 °C for SSU, and 58°C for TEF. PCR amplicons were visualized under UV light on 1.2% agarose gels stained with GoldView (TM) Gel Stain. The PCR

TABLE 1. Details of *Camarosporidiella* species included in the phylogenetic study.

SPECIES	CULTURE NO ^a	SPECIMEN NO ^b	HOST / SUBSTRATE	COUNTRY	GENBANK ACCESSION NO. ^c			
					ITS	LSU	SSU	TEF
<i>C. aborescentis</i>	CPC 31420	–	<i>Cytisus borysthenicus</i>	Ukraine	KY929127	KY929163	—	—
	MFLUCC 14-0604	–	<i>Colutea arborescens</i>	Russia	KP711377	KP711378	KP711379	—
	–	MFLU 15-2181	<i>Colutea orientalis</i>	Russia	MF434115	MF434202	MF434290	MF434378
	MFLUCC 17-0660	MFLU 15-3630	<i>Colutea arborescens</i>	Italy	MF434116	MF434203	MF434291	MF434379
	MFLUCC 17-0738	MFLU 16-2387	<i>Amorpha</i> sp.	Russia	MF434117	MF434204	MF434292	MF434380
<i>C. arezzoensis</i>	MFLUCC 14-0891	MFLU 17-0455	<i>Amorpha fruticosa</i>	Russia	MF434118	MF434205	MF434293	MF434381
	MFLUCC 14-0899 = CBS 143102	MFLU 17-0462	<i>Cytisus austriacus</i>	Russia	MF434119	MF434206	MF434294	MF434382
	MFLUCC 14-0913 = CBS 143103	MFLU 17-0475	<i>Cytisus borysthenicus</i>	Russia	MF434120	MF434207	MF434295	MF434383
	MFLUCC 14-0916 = CBS 143104	MFLU 17-0478	<i>Cytisus austriacus</i>	Russia	MF434121	MF434208	MF434296	MF434384
	MFLUCC 14-0238	MFLU14-0636	<i>Cytisus</i> sp.	Italy	—	KP120927	KP120928	—
	MFLUCC 14-0605	MFLU 14-0794	<i>Caragana frutex</i>	Russia	KP711380	KP711381	KP711382	—
	MFLUCC 14-0887 = CBS 143105	MFLU 17-0453	<i>Caragana frutex</i>	Russia	MF434122	MF434209	MF434297	MF434385
	MFLUCC 14-0896 = CBS 143106	MFLU 17-0459	<i>Caragana frutex</i>	Russia	MF434123	MF434210	MF434298	MF434386
<i>C. caraganicola</i>	MFLUCC 17-0697 = CBS 143107	MFLU 15-2242	<i>Caragana frutex</i>	Russia	MF434124	MF434211	MF434299	MF434387
	MFLUCC 17-0726 = CBS 143108	MFLU 16-1782	<i>Caragana frutex</i>	Russia	MF434125	MF434212	MF434300	MF434388
	MFLUCC 18-0786	MFLU 17-2539	<i>Amorpha fruticosa</i>	Ukraine	MN244227	MN244210	—	MN587129
	–	MFLU 15-3551	Unidentified stem	Italy	—	MF434213	MF434301	—
	MFLUCC 15-0444	–	<i>Celtis occidentalis</i>	Russia	KU697613	KU697614	KU697615	KU697612
	–	MFLU 15-1897	<i>Spiraea</i> sp.	Russia	MF434126	MF434214	MF434302	MF434389
	–	MFLU 15-2036	<i>Elymus repens</i>	Russia	MF434127	MF434215	MF434303	MF434390
	MFLUCC 14-0884 = CBS 143109	MFLU 17-0450	<i>Maclura pomifera</i>	Russia	MF434128	MF434216	MF434304	MF434391
<i>C. celtidis</i>	MFLUCC 14-0904 = CBS 143110	MFLU 17-0466	<i>Gleditsia triacanthos</i>	Russia	MF434129	MF434217	MF434305	MF434392

SPECIES	CULTURE NO ^a	SPECIMEN NO ^b	HOST / SUBSTRATE	COUNTRY	GENBANK ACCESSION NO. ^c			
					ITS	LSU	SSU	TEF
<i>C. clematidis</i> <i>C. elaeagnicola</i>	MFLUCC 17-0556	MFLU 15-2062	<i>Betula pendula</i>	Russia	MF434130	MF434218	MF434306	MF434393
	MFLUCC 17-0676 = CBS 143111	MFLU 15-1928	<i>Prunus padus</i>	Russia	MF434131	MF434219	MF434307	MF434394
	MFLUCC 17-0679	MFLU 15-1943	<i>Morus alba</i>	Russia	MF434132	MF434220	MF434308	MF434395
	MFLUCC 17-0701 = CBS 143112	MFLU 15-2912	<i>Ailanthus altissima</i>	Russia	MF434133	MF434221	MF434309	MF434396
	MFLUCC 17-0735	MFLU 16-2358	<i>Robinia</i> sp.	Russia	MF434134	MF434222	MF434310	MF434397
	MFLUCC 18-1134	MFLU 17-2492	<i>Ulmus pumila</i>	Ukraine	MN244225	MN244208	MN244185	—
	MFLUCC 13-0336	MFLU13-0336	<i>Clematis vitalba</i>	Italy	KJ562213	KJ562188	KJ589414	—
	—	MFLU 15-1924	<i>Artemisia santonicum</i>	Russia	MF434135	MF434223	MF434311	MF434398
	—	MFLU 15-2215	<i>Elaeagnus angustifolia</i>	Russia	MF434136	MF434224	MF434312	MF434399
	MFLUCC 14-0908 = CBS 143113	MFLU 17-0470	<i>Elaeagnus angustifolia</i>	Russia	MF434137	MF434225	MF434313	MF434400
	MFLUCC 14-0911 = CBS 143114	MFLU 17-0473	<i>Elaeagnus angustifolia</i>	Russia	MF434138	MF434226	MF434314	MF434401
	MFLUCC 14-0912 = CBS 143115	MFLU 17-0474	<i>Elaeagnus angustifolia</i>	Russia	MF434139	MF434227	MF434315	MF434402
	MFLUCC 17-0705	MFLU 15-2956	<i>Elaeagnus angustifolia</i>	Russia	MF434140	MF434228	MF434316	MF434403
	MFLUCC 17-0706	MFLU 15-2958	<i>Elaeagnus angustifolia</i>	Russia	MF434141	MF434229	MF434317	MF434404
	MFLUCC 17-0707	MFLU 15-2962	<i>Elaeagnus angustifolia</i>	Russia	MF434142	MF434230	MF434318	MF434405
	MFLUCC 17-0712	MFLU 16-1481	<i>Elaeagnus angustifolia</i>	Russia	MF434143	MF434231	MF434319	MF434406
	MFLUCC 17-0737	MFLU 16-2382	<i>Elaeagnus angustifolia</i>	Russia	MF434144	MF434232	MF434320	MF434407
	CPC 31031		<i>Elaeagnus rhamnoides</i>	Germany	KY929131	KY929166	—	—
	MFLUCC 18-0782	MFLU 17-2505	<i>Cytisus ruthenicus</i>	Ukraine	MN244226	MN244209	MN244186	—
	MFLUCC 18-0788	MFLU 17-2551	<i>Elaeagnus angustifolia</i>	Ukraine	MN244228	MN244211	MN244187	MN587132
	MFLUCC 18-0764	MFLU 17-1849	<i>Elaeagnus angustifolia</i>	Russia	—	MN244212	MN244188	MN587133
<i>C. elongata</i>	CBS 171.55	—	<i>Robinia pseudoacacia</i>	Germany	—	DQ678061	DQ678009	DQ677904
	MFLUCC 14-0260	—	<i>Cytisus scoparius</i>	Germany	—	KJ724249	—	—
<i>C. eufemiana</i>	MFLUCC 17-0207 = CBS 143116	MFLU 16-0182	<i>Cytisus</i> sp.	Italy	MF434145	MF434233	MF434321	MF434408
<i>C. halimodendri</i>	MFLUCC 14-0901 = CBS 143117	MFLU 17-0463	<i>Caragana halodendron</i>	Russia	MF434146	MF434234	MF434322	MF434409

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					ITS	LSU	SSU	TEF
<i>C. italica</i>	MFLUCC 14-0905	MFLU 17-0467	<i>Caragana halodendron</i>	Russia	MF434147	MF434235	MF434323	MF434410
	MFLUCC 14-0907 = CBS 143118	MFLU 17-0469	<i>Caragana frutex</i>	Russia	MF434148	MF434236	MF434324	MF434411
	MFLUCC 14-0914	MFLU 17-0476	<i>Cytisus podolicus</i>	Russia	MF434149	MF434237	MF434325	MF434412
	MFLUCC 17-0212 = CBS 143119	MFLU 15-2123	<i>Lycium barbarum</i>	Russia	MF434150	MF434238	MF434326	MF434413
	MFLUCC 17-0691	MFLU 15-2172	<i>Caragana halodendron</i>	Russia	MF434151	MF434239	MF434327	MF434414
	MFLUCC 18-0767	MFLU 17-2008	<i>Robinia pseudoacacia</i>	Russia	MN244235	MN244219	MN244195	—
	MFLUCC 13-0547	MFLU 17-0139	<i>Hippocrepis emerus</i>	Italy	MF434152	MF434240	MF434328	MF434415
	MFLUCC 14-0885	MFLU 17-0451	<i>Laburnum anagyroides</i>	Russia	MF434153	MF434241	MF434329	MF434416
	MFLUCC 14-0919 = CBS 143121	MFLU 16-0094	<i>Laburnum anagyroides</i>	Italy	MF434154	MF434242	MF434330	MF434417
	MFLUCC 17-0704 = CBS 143122	MFLU 15-2954	<i>Laburnum anagyroides</i>	Russia	MF434155	MF434243	MF434331	MF434418
<i>C. laburni</i>	MFLUCC 17-0709	MFLU 15-2981	<i>Laburnum</i> sp.	Russia	MF434156	MF434244	MF434332	MF434419
	MFLUCC 17-0751 = CBS 143120	MFLU 17-1434	<i>Laburnum anagyroides</i>	Russia	MF434157	MF434245	MF434333	MF434420
	MFLUCC 17-0752	MFLU 17-1435	<i>Laburnum anagyroides</i>	Russia	MF434158	MF434246	MF434334	MF434421
	MFLUCC 14-0565	MFLU 15-1522	<i>Laburnum anagyroides</i>	Russia	:KY497784	KY497779	KY497781	KY497785
	MFLUCC 14-0883 = CBS 143123	MFLU 17-0449	<i>Caragana arborescens</i>	Russia	MF434159	MF434247	MF434335	MF434422
	MFLUCC 14-0893 = CBS 143124	MFLU 17-0457	<i>Caragana arborescens</i>	Russia	MF434160	MF434248	MF434336	MF434423
	MFLUCC 17-0703	MFLU 15-2953	<i>Caragana</i> sp.	Russia	MF434161	MF434249	MF434337	MF434424
	CPC 25960		<i>Caragana</i> sp.	Finland	KY929129	KY929164	—	KY929198
	CPC 25962		<i>Caragana</i> sp.	Finland	KY929130	KY929165		KY929199
	MFLUCC 17-0684	MFLU 15-2022	<i>Caragana frutex</i>	Russia	MF434162	MF434250	MF434338	MF434425
<i>C. melnikii</i>	—	MFLU 17-228	<i>Robinia pseudoacacia</i>	Russia	MF434163	MF434251	MF434339	MF434426
<i>C. mirabellensis</i>	—	MFLU 17-2147	<i>Morus alba</i>	Russia	MK590359	MK590358	—	—
<i>C. mori</i>	—	MFLU 15-1936	<i>Morus alba</i>	Russia	MF434164	MF434252	MF434340	MF434427
<i>C. moricola</i>	—	MFLU 15-2223	<i>Morus alba</i>	Russia	MF434165	MF434253	MF434341	MF434428
	MFLUCC 14-0886	MFLU 17-0452	<i>Morus alba</i>	Russia	MF434166	MF434254	MF434342	MF434429

SPECIES	CULTURE NO ^A	SPECIMEN NO ^B	HOST / SUBSTRATE	COUNTRY	GENBANK ACCESSION NO. ^C			
					ITS	LSU	SSU	TEF
<i>C. populina</i>	MFLUCC 14-0898	MFLU 17-0461	<i>Morus alba</i>	Russia	MF434167	MF434255	MF434343	MF434430
	MFLUCC 16-1396	MFLU 15-2075	<i>Morus alba</i>	Russia	KY053887	KY053890	KY053893	—
	MFLUCC 16-1397	MFLU 15-2222	<i>Morus alba</i>	Russia	KY053888	KY053891	KY053894	—
	MFLUCC 16-1398	MFLU 15-2223	<i>Morus alba</i>	Russia	KY053889	KY053892	KY053895	—
	MFLUCC 17-0680	MFLU 15-1969	<i>Morus alba</i>	Russia	MF434168	MF434256	MF434344	MF434431
	MFLUCC 17-0687	MFLU 15-2075	<i>Morus alba</i>	Russia	MF434169	MF434257	MF434345	MF434432
	MFLUCC 17-0694	MFLU 15-2222	<i>Morus alba</i>	Russia	MF434170	MF434258	MF434346	MF434433
	MFLUCC 17-0711	MFLU 15-2999	<i>Morus alba</i>	Russia	MF434171	MF434259	MF434347	MF434434
	MFLUCC 17-0714 = CBS 143125	MFLU 16-1527	<i>Morus alba</i>	Russia	MF434172	MF434260	MF434348	MF434435
	MFLUCC 17-0718 = CBS 143126	MFLU 16-1626	<i>Morus alba</i>	Russia	MF434173	MF434261	MF434349	MF434436
	MFLUCC 17-0719	MFLU 16-1639	<i>Morus alba</i>	Russia	MF434174	MF434262	MF434350	MF434437
	MFLUCC 17-0725	MFLU 16-1770	<i>Morus alba</i>	Russia	MF434175	MF434263	MF434351	MF434438
	MFLUCC 18-0766	MFLU 17-1904	<i>Morus alba</i>	Russia	MN244229	MN244213	MN244189	—
	MFLUCC 18-0768	MFLU 17-2010	<i>Morus alba</i>	Russia	MN244230	MN244214	MN244190	MN587134
	MFLUCC 18-0769	MFLU 17-2035	<i>Morus alba</i>	Russia	MN244231	MN244215	MN244191	MN587135
	MFLUCC 18-0770	MFLU 17-2036	<i>Morus alba</i>	Russia	MN244232	MN244216	MN244192	MN587136
	MFLUCC 18-0771	MFLU 17-2060	<i>Morus alba</i>	Russia	MN244233	MN244217	MN244193	MN587137
	MFLUCC 18-0772	MFLU 17-2085	<i>Morus alba</i>	Russia	MN244234	MN244218	MN244194	—
	MFLUCC 17-2310	MFLU 17-0991	<i>Morus nigra</i>	Italy	MN603933	MN608782	—	MN587138
	MFLUCC 18-0087	MFLU 16-1722	<i>Populus nigra</i>	Russia	NR_161040	—	NG_065721	—
	<i>C. premilcurensis</i>	MFLUCC 17-0208 = CBS 143127	<i>Cytisus</i> sp.	Italy	MF434176	MF434264	MF434352	MF434439
	<i>C. robinicola</i>	MFLUCC 13-0527	<i>Robinia pseudoacacia</i>	Italy	KJ562214	KJ589412	KJ589415	—
	MFLUCC 14-0892 = CBS 143128	MFLU 17-0456	<i>Gleditsia triacanthos</i>	Russia	MF434177	MF434265	MF434353	MF434440
	MFLUCC 14-0894 = CBS 143129	MFLU 17-0458	<i>Robinia neomexicana</i>	Russia	MF434178	MF434266	MF434354	MF434441
	MFLUCC 14-0906 = CBS 143130	MFLU 17-0468	<i>Gleditsia triacanthos</i>	Russia	MF434179	MF434267	MF434355	MF434442

SPECIES	CULTURE NO ^a	SPECIMEN NO ^b	HOST / SUBSTRATE	COUNTRY	GENBANK ACCESSION NO. ^c			
					ITS	LSU	SSU	TEF
<i>C. schulzeri</i>	MFLUCC 14-0909 = CBS 143131	MFLU 17-0471	<i>Robinia pseudoacacia</i>	Russia	MF434180	MF434268	MF434356	MF434443
	MFLUCC 17-0688	MFLU 15-2104	<i>Robinia pseudoacacia</i>	Russia	MF434181	MF434269	MF434357	MF434444
	MFLUCC 17-0716 = CBS 143132	MFLU 16-1597	<i>Robinia</i> sp.	Russia	MF434182	MF434270	MF434358	MF434445
	MFLUCC 17-0733	MFLU 16-2300	<i>Robinia</i> sp.	Russia	MF434183	MF434271	MF434359	MF434446
	CPC 27667	—	<i>Robinia pseudoacacia</i>	Ukraine	KY929133	KY929168	—	—
	CPC 30379	—	<i>Philadelphus coronarius</i>	Germany	KY929134	KY929169	—	—
	MFLUCC 18-0775	MFLU 17-2469	<i>Robinia pseudoacacia</i>	Ukraine	MN244236	MN244220	MN244196	MN587130
	MFLUCC 18-0789	MFLU 18-0320	<i>Robinia pseudoacacia</i>	Russia	MN244224	MN244207	MN244184	MN587131
	MFLUCC 14-0620	MFLU 14-0770	<i>Cotinus coggygria</i>	Russia	KP744436	KP744478	KP753948	
	—	MFLU 15-1909	<i>Gleditsia triacanthos</i>	Russia	MF434184	MF434272	MF434360	MF434447
	MFLUCC 14-0897 = CBS 143133	MFLU 17-0460	<i>Elaeagnus angustifolia</i>	Russia	MF434185	MF434273	MF434361	MF434448
	MFLUCC 17-0717	MFLU 16-1599	<i>Robinia</i> sp.	Russia	MF434186	MF434274	MF434362	MF434449
	MFLUCC 17-0722	MFLU 16-1664	<i>Robinia</i> sp.	Russia	MF434187	MF434275	MF434363	MF434450
<i>Camarosporidiella</i> sp.	CPC 31632	—	<i>Ulmus laevis</i>	Ukraine	KY929132	KY929132	—	—
<i>Camarosporidiella</i> sp.	CPC 12441	—	<i>Sophora chrysophylla</i>	Hawaii	KY929128	DQ377885	—	—
<i>C. spartii</i>	MFLUCC 14-0915	MFLU 17-0477	<i>Cytisus ruthenicus</i>	Russia	MF434188	MF434276	MF434364	MF434451
	MFLUCC 17-0713 = CBS 143134	MFLU 16-1484	<i>Bassia</i> sp.	Russia	MF434189	MF434277	MF434365	MF434452
	MFLUCC 13-0548	—	<i>Cytisus</i> sp.	Italy	KJ562215	—	—	—

^a Culture Collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; MFLUCC: Mae Fah Luang University

^b Culture Collection, Chiang Rai, Thailand. MFLU: Mae Fah Luang University (MFLU) Herbarium, Chiang Rai, Thailand; TASM: Tashkent Mycological Herbarium, Institute of Botany and Zoology, Academy of Sciences of Uzbekistan, Tashkent, Uzbekistan.

^c ITS: Internal transcribed spacers; LSU: partial 28S nrDNA; SSU: partial 18S nrDNA; TEF: translation elongation factor 1-alpha gene. Newly generated sequences are shown in bold.

amplification products (amplimers) were analysed by the BGI, Ltd (Shenzhen, PR China). Same primer pairs used for amplification process were used for sequencing. The nucleotide sequences were deposited in GenBank (TABLE 1), and the final alignment and tree are deposited in TreeBASE (<http://www.treebase.org/>).

Phylogenetic and sequence analysis

The raw trace files were edited using BioEdit v. 7.0.5.2 (Hall 1999) and unclear peaks were omitted from the beginning and end of the sequences. A consensus sequence was generated manually for each set of trace files from the forward and reverse sequences, which were subjected to standard GenBank BLAST searches to compare with other fungal DNA sequences from NCBI's GenBank sequence database. High similarity sequences were added to the alignments. Sequences generated in this study and those obtained from GenBank were aligned using MAFFT (Kuraku & al. 2013, Katoh & al. 2017) and adjusted visually in BioEdit v. 7.0.5.2. The best evolutionary model for each data partition was obtained using MrModelTest v. 2.3 (Nylander 2004) under the Akaike Information Criterion (AIC) implemented in both PAUP v. 4.0b10 and MrBayes v. 3. The combined gene trees were phylogenetically regenerated using both Bayesian Inference (BI) and Maximum Likelihood (ML) criteria as outlined in Jeewon & al. (2017), Pem & al. (2019a,b), and Senanayake & al. (2017). ML analysis was conducted in RAXML-HPC2 on XSEDE (8.2.8) (Stamatakis 2006) implemented in raxmlGUI v.0.9b2 (Silvestro & Michalak 2012), employing GTR+I+G evolutionary settings; bootstrap support values were obtained by running 1000 pseudo replicates. Bayesian inference (BI) analysis was run with MrBayes v. 3.2.1 (Ronquist & Huelsenbeck 2003) to evaluate Posterior probabilities (BYPP) (Rannala & Yang 1996, Zhaxybayeva & Gogarten 2002) with Markov Chain Monte Carlo (MCMC) sampling. The heating parameter was set at 0.15. Two parallel runs were conducted using the default settings. The analysis lasted until the average standard deviation of split frequencies came below 0.01. Trees were saved each 1000 generation, with the first 25% discarded as the 'burn-in' phase. BYPP were calculated from the remaining trees. The resulting phylogenetic tree was visualized with FigTree v1.4.0 program (Rambaut 2012) and reorganized in Microsoft Power Point 2007 and Adobe Illustrator CS5 (v. 15.0.0). Sequences generated in this study were submitted to NCBI's GenBank nucleotide database (<http://www.ncbi.nlm.nih.gov>; TABLE 1).

Phylogenetic results

Topologies of ML and BI trees recovered for each gene dataset were visually compared, and the overall tree topology was congruent to those obtained from the combined dataset. The RAXML analysis of the combined dataset yielded a best scoring tree (FIG. 1a,b,c) with a final ML optimization likelihood value of -7746.830774 . The matrix had 412 distinct alignment patterns, with 11.62% proportion of gaps and completely undetermined characters in this alignment. Parameters for the GTR + I + G model of

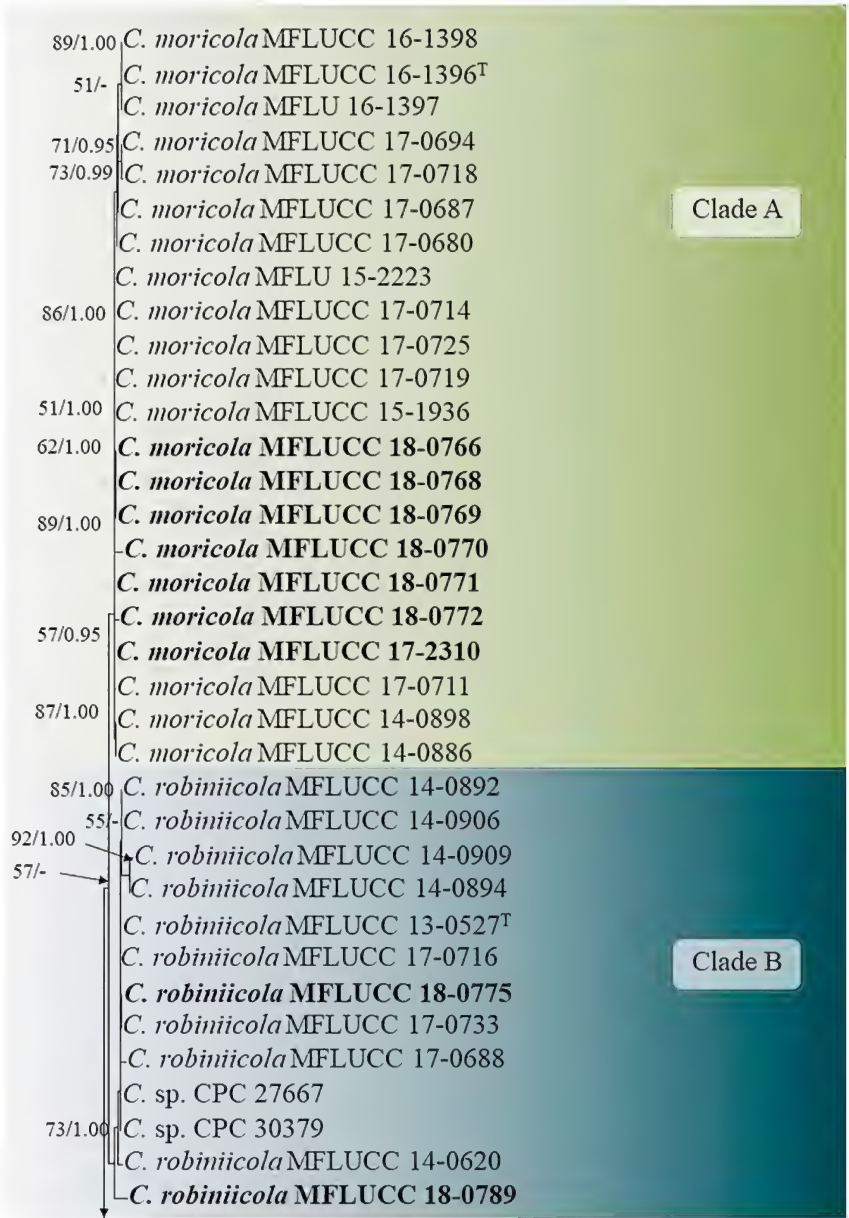
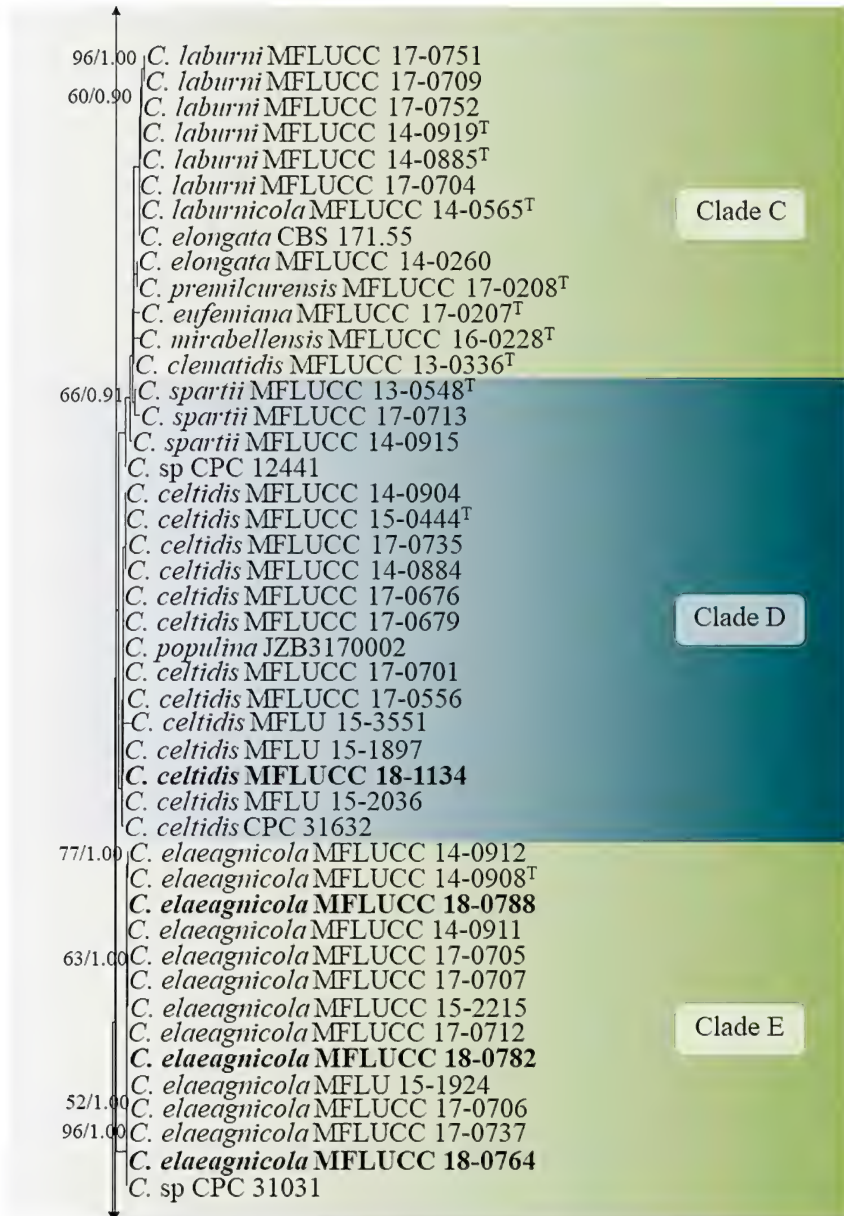
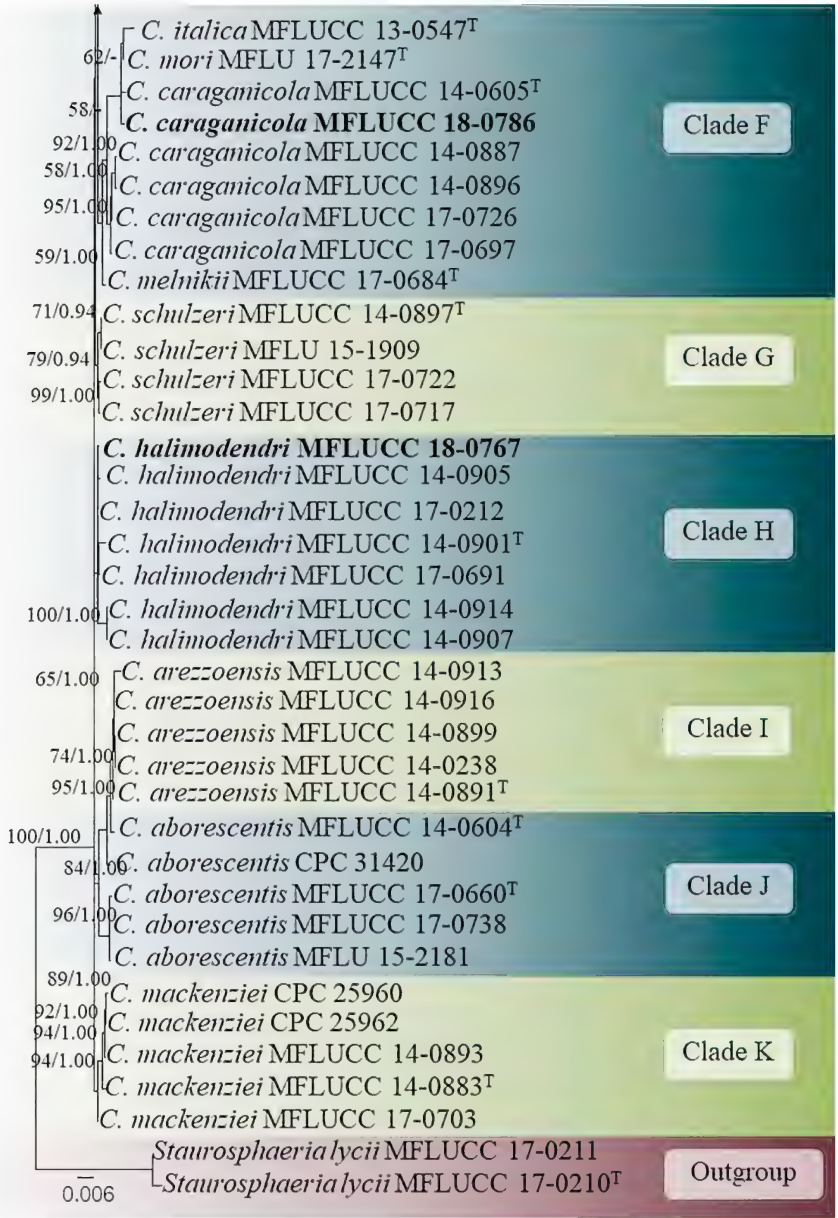


FIG. 1a–c (pp.460–462). RAxML tree of *Camarosporidiella* spp. based on analysis of a combined dataset of LSU, SSU, ITS, and TEF partial sequence data. Bootstrap support values for ML $\geq 50\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are presented as ML/PP above and below the



nodes. The new isolates are set in bold font. Ex-type strains are indicated with a superscript ^T. The scale bar represents the expected number of nucleotide substitutions per site.



the combined LSU, ITS, SSU and TEF were as follows: Estimated base frequencies: A = 0.243219, C = 0.241435, G = 0.266791, T = 0.248554; substitution rates AC = 1.018686, AG = 2.994042, AT = 1.771673, CG = 1.029209, CT = 4.405919, GT = 1.000000; proportion of invariable sites I = 0.845457; gamma distribution shape parameter α = 0.909328. The Bayesian analysis resulted in 10,000 trees after 1 M generations with 0.049881 as the average standard deviation of split frequency. The first 2000 trees representing the burn-in phase of the analyses were discarded, and the remaining 8000 trees were used for calculating posterior probabilities in the majority rule consensus tree.

Newly generated sequences from seven *Camarosporidiella* isolates (MFLUCC 18-0766, MFLUCC 18-0768, MFLUCC 18-0769, MFLUCC 18-0770, MFLUCC 18-0771, MFLUCC 18-0772, and MFLUCC 17-2310) grouped with isolates previously circumscribed as *C. moricola* (Wanasinghe & al. 2017, Tibpromma & al. 2017). These sequences formed a distinct clade (FIG. 1, CLADE A) within *Camarosporidiella*, but were poorly supported in multi-gene analyses (MI = 62%, BI = 1; and ML = 89%, BI = 1). Two other isolates (MFLUCC 18-0775 and MFLUCC 18-0789) showed a close phylogenetic affinity with *C. robinicola* strains and two unidentified *Camarosporidiella* species (CPC 27667 and CPC 30379); this relationship retrieved a support of ML = 73%, BI = 1 (FIG. 1, CLADE B). Isolate MFLUCC 18-1134 clustered with *C. celtidis* strains (FIG. 1, CLADE D). Three newly generated sequences, MFLUCC 18-0764, MFLUCC 18-0782, and MFLUCC 18-0788 grouped with *C. elaeagnicola* isolates with statistical support (ML = 60%, BI = 1). (FIG. 1, CLADE E). Isolate MFLUCC 18-0786 clustered with *C. caraganicola* (MFLUCC 14-0605), *C. mori* (MFLU 17-2147), and *C. italica* (MFLUCC 13-0547) (FIG. 1, CLADE F). MFLUCC 18-0767 nested among *C. halimodendri* isolates including ex-type strain (MFLUCC 14-0901) (FIG. 1, CLADE H).

Taxonomy

Camarosporidiella caraganicola (Phukhams., Bulgakov & K.D. Hyde)

Phukhams., Wanas. & K.D. Hyde, Stud. Mycol. 87: 220 (2017)

PLATE 1, FIG. 2e,f

SAPROBIC on dead branches of *Amorpha fruticosa* L. (*Fabaceae*). SEXUAL MORPH: ASCOMATA 200–380 μ m high, 250–380 μ m diam. ($x = 333.4 \times 286.1$ μ m, $n = 10$), black, superficial to semi-immersed, in groups, occasionally dispersed underneath the host periderm, entirely or moderately erumpent,



PLATE. 1. *Camarosporidiella caraganicola* (MFLU 17-2539). a, b. Ascomata on host surface; c. Ascoma, vertical section; d, e. Peridium; f. Hamathecium; g-j. Asci; k-r. Ascospores. Scale bars: a = 1000 μ m; b = 500 μ m; c = 200 μ m; d, e = 25 μ m; f = 5 μ m; g-j = 50 μ m; k-r = 10 μ m.

globose, rough, ostiolate. OSTIOLE central, short, slightly sunken, tiny, inconspicuous on surface, smooth, with ostiolar canal filled with hyaline cells. PERIDIUM 80–90 μ m at the base, 60–90 μ m on the sides, comprising 3–4 layers, with outer layer cells heavily pigmented, thick-walled, dark brown

cells of a *textura angularis* and the cells towards the inside lightly coloured with an inner layer comprising 3–4 layers, hyaline, flattened, thin-walled, a *textura angularis*. HAMATHECIUM comprising numerous pseudoparaphyses 2.8–3.6 μm ($n = 20$) diam., filamentous, branched, septate. ASCI 150–180 $\times$ 10–12 μm ($x = 163.8 \times 11.7 \mu\text{m}$, $n = 30$), 8-spored, bitunicate, fissitunicate, cylindrical, short-pedicellate, rounded at apex with a tiny ocular chamber. ASCOSPORES 20–24 $\times$ 7–8 μm ($x = 22.9 \times 7.3 \mu\text{m}$, $n = 50$), overlapping uniseriate, muriform, ellipsoidal, 3–5-transversely septate, with 2–4 vertical septa, constricted at middle septum, initially hyaline and becoming brown at maturity, marginally paler, pointed and narrow at the ends, not surrounded by a mucilaginous sheath.

CULTURE CHARACTERISTICS: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with dense mycelium, circular, rough margin, hairy, white at first, greenish grey after 2 months, reverse greenish grey in the middle, whitish at the margin, flat on the surface.

SPECIMEN EXAMINED: UKRAINE, DONETSK REGION, Donetsk city, Donetsk Botanical Garden, lower park near pond, dying and dead twigs of *Amorpha fruticosa*, 20 May 2017, Timur S. Bulgakov (MFLU 17-2539; living cultures MFLUCC 18-0786, DSM 109978).

NOTES: Our specimen of *Camarosporidiella caraganicola* is morphologically and phylogenetically similar to another specimen collected from a different host, *Caragana frutex* (L.) K. Koch (*Fabaceae*); we isolated our strain from *Amorpha fruticosa*. Liu & al. (2015) reported the asexual morph, and Wanasinghe & al. (2017) reported the sexual morph. The phylogenetic placement of our strain (MFLUCC 18-1128) is shown in FIG. 1.

HOSTS: *Caragana frutex* (Liu & al. 2015, Wanasinghe & al. 2017); *Amorpha fruticosa* (this study).

DISTRIBUTION: Russia: Liu & al. 2015, Wanasinghe & al. 2017; Ukraine: this study).

Camarosporidiella celtidis (Shear) Thambug., Wanas. & K.D. Hyde,

Stud. Mycol. 87: 226 (2017)

PLATE 2, FIG. 2c,d

SAPROBIC on dead twigs of *Ulmus pumila* L. (*Ulmaceae*).

ASEXUAL MORPH: CONIDIOMATA 250–350 μm high, 220–470 μm diam. ($x = 280.5 \times 314.7 \mu\text{m}$, $n = 10$), solitary or gregarious, black, immersed to semi-immersed, unilocular, ostiolate. CONIDIOMATAL WALL 25–50 μm thick at the base, 25–35 μm and thick at the sides, comprising 3–4 layers, outer layer heavily pigmented, thick-walled, comprising dark reddish-brown cells of *textura angularis*, cells towards the inside lighter with the inner layer comprising 3–4 layers, hyaline, with thick-walled cells of *textura*

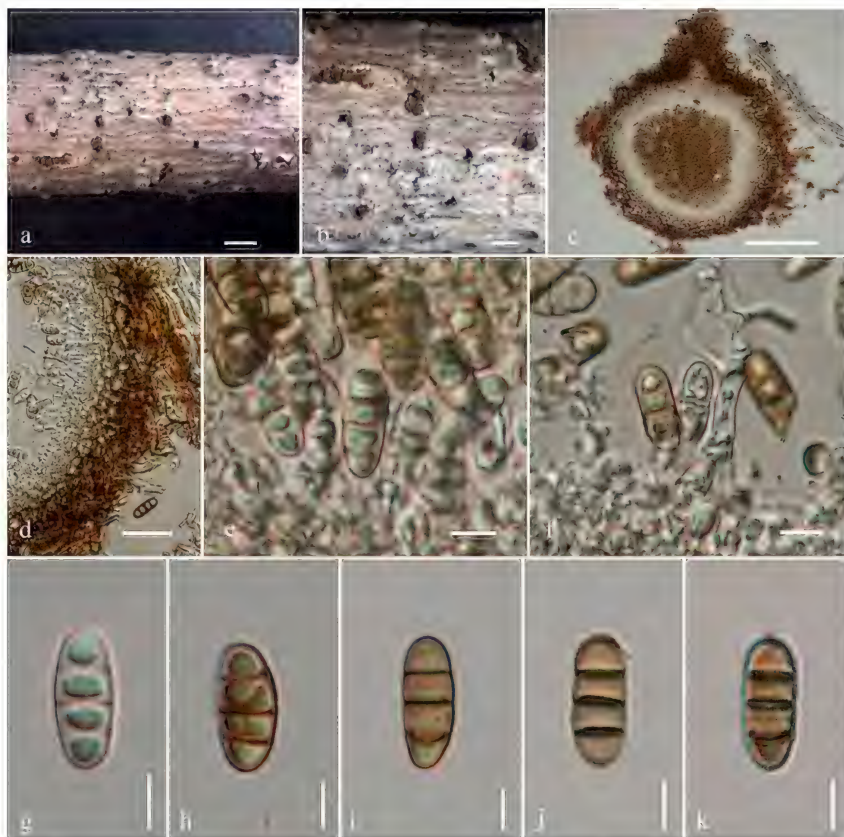


PLATE. 2. *Camarosporidiella celtidis* (MFLU 17-2492). a, b. Conidiomata on host surface; c. Conidioma, vertical section; d. Peridium; e–f. Conidiogenous cells and developing conidia; g–k. Conidia. Scale bars: a, b = 500 μ m; c = 100 μ m; d = 30 μ m; e–k = 5 μ m.

angularis. OSTIOLE 25–30 μ m long, 30–40 μ m diam. ($x = 26.5 \times 37.5 \mu$ m, $n = 6$), central, smooth, ostiolar canal filled with hyaline or pale brown cells. CONIDIOPHORES reduced to conidiogenous cells. CONIDIEXOGENOUS CELLS enteroblastic, annellidic, doliiform, integrated, solitary, hyaline, smooth-walled, and formed from the inner layer of conidiomatal wall. CONIDIA 9–14 $\times$ 4–5 μ m ($x = 12.3 \times 5.0 \mu$ m, $n = 40$), oblong, straight, rounded at both ends, 2–3-transversely euseptate, without vertical septa, smooth-walled, slightly constricted at septa, initially hyaline, becoming brown to dark brown at maturity.

CULTURE CHARACTERISTICS: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with medium dense mycelium, circular smooth entire margin, radially furrowed, hairy, white at first, yellowish white after 2 months, reverse off white in the middle, white at the margin, flat on the surface.

SPECIMEN EXAMINED: UKRAINE, DONETSK REGION, Shakhtyorsk district, “Donetsk Ridge” regional landscape park (“Donetskiy kryazh”), old artificial forest belt, on *Ulmus pumila*, 19 May 2017, Timur S. Bulgakov (MFLU 17-2492; living cultures MFLUCC 18-1134, DSM 109786).

NOTES: Our isolate MFLUCC 18-1134 clustered with the ex-type strain of *Camarosporidiella celtidis*, previously described by Wanasinghe & al. (2017). The main difference between descriptions by Wanasinghe & al. (2017) and our *C. celtidis* isolate is the size of conidia (15–20 × 6–8 µm vs. 9–14 × 4–5 µm). However, our LSU, SSU, ITS, and TEF sequence analyses showed a 100% similarity between our isolate and the other *C. celtidis* isolates in GenBank. In view of the phylogenetic and morphological similarities, we introduce our collection as a new record on *Ulmus pumila*.

HOSTS: *Ailanthus altissima* (Mill.) Swingle, *Betula pendula* Roth, *Celtis occidentalis* L., *Elymus repens* (L.) Gould, *Gleditsia triacanthos* L., *Maclura pomifera* (Raf.) C.K. Schneid., *Morus alba* L., *Prunus padus* L., *Spiraea* sp., (Thambugala & al. 2016, Wanasinghe & al. 2017); *Ulmus pumila* (this study).

DISTRIBUTION: Russia (Thambugala & al. 2016, Wanasinghe & al. 2017); Ukraine (this study).

Camarosporidiella elaeagnicola Wanas., Bulgakov & K.D. Hyde,

Stud. Mycol. 87: 227 (2017)

PLATE 3, FIG. 2g,h

NECROTROPHIC on dying twigs.

SEXUAL MORPH: Undetermined.

ASEXUAL MORPH: CONIDIOMATA pycnidial, 170–270 µm high, 180–330 µm diam. ($x = 259.4 \times 204.6$ µm, $n = 10$), solitary or gregarious, black, immersed to slightly erumpent, unilocular, ostiolate. OSTIOLE 17–20 µm long, 19–25 µm diam. ($x = 15.2 \times 19.1$ µm, $n = 10$), central, smooth, ostiolar canal filled with hyaline or pale brown cells. CONIDIOMATAL WALL multi-layered, 25–35 µm thick at the base, 35–50 µm thick at the sides, comprising 5–8 layers of heavily pigmented dark brown cells of textura angularis, with lighter cells towards the inside, with inner layer comprising 2–4 layers, cells a textura angularis, hyaline, thin-walled. MACROCONIDIOPHORES reduced to conidiogenous cells. MACROCONIDIOGENOUS CELLS enteroblastic with percurrent annellations, doliiform, integrated, solitary, hyaline, smooth-walled, and formed from the inner layer of conidiomatal wall.

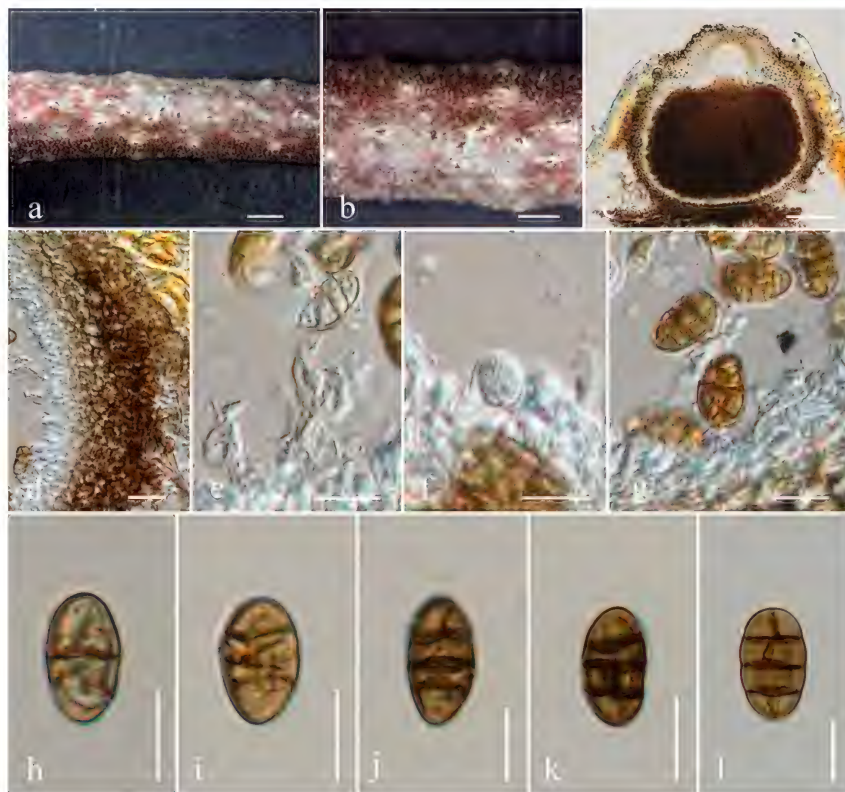


PLATE. 3. *Camarosporidiella elaeagnicola* (MFLU 17-2505). a, b. Conidiomata on host surface; Conidioma, vertical section; d. Peridium; e–g. Conidiogenesis; h–l. Conidia. Scale bars: a = 1000 μm ; b = 500 μm ; c = 25 μm ; d = 20 μm ; e–l = 10 μm .

MACROCONIDIA 13–18 $\times$ 8–9 μm ($\bar{x}$ = 15.5 $\times$ 9.0 μm , n = 30), ellipsoidal, straight to slightly curved, rounded at both ends, 2–3-transversely septate, with 2–4 vertical septa, muriform, smooth, pale to dark brown.

CULTURE CHARACTERISTICS: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with dense mycelium, circular, smooth well-defined margin, hairy, white at the centre, greenish grey towards margin, reverse greenish grey, flat on the surface.

SPECIMENS EXAMINED: UKRAINE, DONETSK REGION, Shakhtyorsk district, “Donetsk Ridge” regional landscape park (“Donetskiy kryazh”), stony steppe, on dying twigs of *Cytisus ruthenicus* Wol. [= *Chamaecytisus ruthenicus* (Wol.) Klásk.], 19 May

2017, Timur S. Bulgakov (MFLU 17-2505; living culture MFLUCC 18-0782, DSM 109783); **Donetsk city**, Donetsk Botanical Garden, arboretum park near the pond, on dead twigs of *Elaeagnus angustifolia*, 21 May 2017, Irina V. Bondarenko-Borisova (MFLU 17-2551; living culture MFLUCC 18-0788, DSM 109784); **RUSSIA, ROSTOV REGION, Shakhty city district**, rock quarry "Stony pond" ("Kamennyy stav"), on dead twigs of *Elaeagnus angustifolia*, 17 April 2017, Timur S. Bulgakov (MFLU 17-1849; living culture MFLUCC 18-0764; DSM 109794).

NOTES: Our isolate MFLUCC 18-0782 clustered with the ex-type strains of *Camarosporidiella elaeagnicola* originally described by Wanasinghe & al. (2017). However, MFLUCC 18-0782 differs from the type strain in its comparatively smaller conidiomata (170–270 µm high, 185–330 µm diam. vs. 300–500 µm high, 300–550 µm diam.) and shorter conidia (13–18 × 8–9 µm vs. 18–25 × 9–13 µm). MFLUCC 18-0782 originates from Ukraine, while the holotype specimen was collected from an adjacent area of Russia. We provide identify this new collection as *C. elaeagnicola* based on its morphology, phylogeny, and host association.

HOSTS: *Artemisia santonicum* (Asteraceae), *Cytisus ruthenicus* [= *Chamaecytisus ruthenicus*] (this study), *Elaeagnus angustifolia* (Wanasinghe & al. 2017).

DISTRIBUTION: Russia (Wanasinghe & al. 2017), Ukraine (this study).

Camarosporidiella halimodendri Wanas., Bulgakov & K.D. Hyde,

Stud. Mycol. 87: 230 (2017)

PLATE 4, FIG. 2a,b

SAPROBIC on dead branches of *Robinia pseudoacacia* L. (Fabaceae).

SEXUAL MORPH: Undetermined.

ASEXUAL MORPH: CONIDIOMATA pycnidial, 340–490 µm high, 440–710 µm diam. ($x = 586.6 \times 396.3$ µm, $n = 10$), solitary or gregarious, black, immersed or semi-immersed, unilocular papillate. OSTIOLE 35–60 µm long, 40–60 µm diam. ($x = 42.5 \times 54.6$ µm, $n = 6$), central, smooth, ostiolar canal filled with hyaline or pale brown cells. CONIDIOMATAL WALL comprising 1–2 layer of hyaline (inner layer) and dark reddish-brown (outer layer) cells of textura angularis. CONIDIOPHORES reduced to conidiogenous cells. MACROCONIDIOGENOUS CELLS enteroblastic, annellidic, doliiform, integrated, solitary, hyaline, smooth-walled, and formed from the inner layer of conidiomatal wall. MACROCONIDIA 11–22 × 5–7 µm ($x = 14.8 \times 6.9$ µm, $n = 20$), oblong, straight to slightly curved, rounded at both ends, 3–7-transversely septate, with 1–2 vertical septa, with 2–3 oblique septa, muriform, smooth-walled, hyaline when immature becoming dark brown on maturity. MICROCONIDIOGENOUS CELLS intermixed with



PLATE. 4. *Camarosporidiella halimodendri* (MFLU 17-2008). a, b. Conidiomata on host surface; Conidioma, vertical section; d. Peridium; e–g. Conidiogenous cells; h–m. Macroconidia; n–s. Microconidia. Scale bars: a, b = 1000 μm ; c = 100 μm ; d = 30 μm ; e–m, o–s = 5 μm ; n = 10 μm .

macroconidiogenous cells, hyaline, distinct, enteroblastic, annellidic, ampulliform to subcylindrical. MICROCONIDIA 6.6–10.4 $\times$ 2.5–3.3 μm ($x = 7.9 \times 3.0 \mu\text{m}$, $n = 20$), hyaline, oblong to ellipsoidal, allantoid, with a few small guttules, smooth-walled.

CULTURE CHARACTERISTICS: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with sparse mycelium, circular, smooth well-defined margin, grey in the middle, white in the edges, reverse cream-grey in the middle, whitish at the edge, flat on the surface.

SPECIMEN EXAMINED: RUSSIA, ROSTOV REGION, Shakhty city district, urban artificial forest, on dying twigs of *Robinia pseudoacacia*, 26 May 2017, Timur S. Bulgakov (MFLU 17-2008; living cultures MFLUCC 18-0767, DSM 109977).

NOTES: Our new isolate MFLUCC 18-0767 shares a close phylogenetic affinity to *Camarosporidiella halimodendri* (MFLUCC 14-0905) in our combined LSU, SSU, ITS, and TEF phylogenetic tree. Our isolate differs slightly morphologically from the type description in microconidial shape and larger size (vs. $4.5\text{--}7.5 \times 3.5\text{--}4.5\ \mu\text{m}$). *Camarosporidiella halimodendri* has not previously been reported from *Robinia pseudoacacia*, reported here as a new host.

HOSTS: *Caragana frutex*, *C. halodendron* (Pall.) Dum. Cours. [$\equiv$ *Halimodendron halodendron* (Pall.) Voss], *Cytisus podolicus* Blocki [$\equiv$ *Chamaecytisus podolicus* (Blocki) Klásk.], *Lycium barbarum* L. (Wanasinghe & al. 2017), *Robinia pseudoacacia* (this study).

DISTRIBUTION: Russia: Wanasinghe & al. 2017, this study.

Camarosporidiella moricola (Chethana, Bulgakov & K.D. Hyde) Wanas. & K.D. Hyde, Stud. Mycol. 87: 238 (2017) PLATE 5, FIG. 2k,l

NECROTROPHIC on dead and dying twigs of *Morus nigra* L. (*Moraceae*).

SEXUAL MORPH: Undetermined.

ASEXUAL MORPH: CONIDIOMATA 110–175 μm diam., 210–290 μm high, pycnidial, solitary, scattered, semi-immersed, unilocular, globose, black, with a papillate ostiole. CONIDIOMATAL WALL 15–30 μm thick at the base, 20–30 μm thick at the sides, multi-layered, outer layer composed of 3–4 layers of thick, dark brown cells; inner 4–6 layers hyaline cells of textura angularis. CONIDIOPHORES reduced to conidiogenous cells. CONIDIOGENOUS CELLS enteroblastic, with percurrent annellations, doliiform, hyaline, smooth-walled, formed from the inner most layer of the conidiomatal wall. CONIDIA $11\text{--}12 \times 4\text{--}5\ \mu\text{m}$ ($x = 11.9 \times 5.3\ \mu\text{m}$, $n = 20$), oblong, ellipsoidal, straight to slightly curved, initially hyaline becoming pale to dark brown at maturity, smooth-walled, rounded at both ends, muriform, 1–3-transversely septate and 1–2 vertical septa.

CULTURE CHARACTERISTICS: Mycelium slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with dense mycelium, circular, fimbriate,



PLATE. 5. *Camarosporidiella moricola* (MFLU 17-0991). a, b. Conidiomata on host surface; c. Conidioma, vertical section; d. Peridium; e–g. Conidiogenous cells and developing conidia; h–m. Conidia. Scale bars: a = 500 μ m; b = 300 μ m; c = 50 μ m; d = 40 μ m; e–g = 5 μ m; h–m = 10 μ m.

rough margin, olivaceous grey in the middle, reverse creamy-white, flat on the surface.

SPECIMENS EXAMINED: ITALY, PROVINCE OF FORLÌ-CESENA, Predappio Alta-Predappio, on dead branch of *Morus nigra*, 5 May 2017, Erio Camporesi (MFLU 17-0991, MFLUCC 17-2310); RUSSIA, ROSTOV REGION, Shakhty city, urban artificial forest, on *Morus alba*, 26 May 2017, Timur S. Bulgakov (MFLU 17-2060; living cultures MFLUCC 18-0771, DSM 109975); Shakhty city district, artificial forest, on dead twigs of *Morus alba*, 11 June 2017, Timur S. Bulgakov (MFLU 17-2036; living cultures MFLUCC 18-0770, DSM 109835); trees near Atukhta river, on dead twigs of *Morus alba*, 1 June 2017, Timur S. Bulgakov (MFLU 17-1904; living cultures MFLUCC 18-0766, DSM 109917); block green belt, on *Morus alba*, 8 May 2017, Timur S. Bulgakov (MFLU 17-2085; living cultures MFLUCC 18-0772, DSM 109795); Hospital park, trees, on dead twigs of *Morus alba*, 3 June 2017, Timur S.

Bulgakov (MFLU 17-2010; living cultures MFLUCC 18-0768, DSM 109792); former Shakhty Forest, artificial forest, on dead twigs of *Morus alba*, 11 June 2017, Timur S. Bulgakov (MFLU 17-2035; living cultures MFLUCC 18-0769, DSM 109976).

NOTES: Multi-gene phylogenetic analyses group MFLU 17-2310, MFLUCC 18-0766, MFLUCC 18-0768, MFLUCC 18-0769, MFLUCC 18-0770, MFLUCC 18-0771, MFLUCC 18-0772 with *Camarosporidiella moricola*. A BLASTn search of LSU, SSU, ITS, TEF sequences places the seven strains at 99–100% similarity with *C. moricola*. The *C. moricola* type strain differs from our specimens in its larger (150–340 µm diam.) conidiomata. *Camarosporidiella moricola* has been described only on *Morus* species from Russia. We examined fresh specimens both from Russia and Italy. We identify our strains as *C. moricola* and report MFLU 17-0991 as new for Italy.

HOSTS: *Morus alba* (Tibpromma & al. 2017, Wanasinghe & al. 2017); *Morus nigra* (this study).

DISTRIBUTION: Russia (Tibpromma & al. 2017, Wanasinghe & al. 2017), Italy (this study).

Camarosporidiella robiniicola (Wijayaw., Camporesi & K.D. Hyde) Wijayaw., Wanas. & K.D. Hyde, Stud. Mycol. 87: 241 (2017) PLATE 6, FIG. 2i,j

NECROTROPHIC on dying and dead branches of *Robinia pseudoacacia*.

SEXUAL MORPH: Undetermined.

ASEXUAL MORPH: CONIDIOMATA pycnidial, 500–700 µm diam., 200–450 µm high, solitary or gregarious, black, immersed, unilocular, papillate. CONIDIOMATAL WALL multi-layered, 20–35 µm thick at the base, 10–25 µm thick at the sides, comprising 4–5 layers of dark brown cells of textura angularis, with lighter cells towards the inside, inner layer composed of 2–4 layers, hyaline, thin-walled cells of textura angularis. CONIDIOPHORES reduced to conidiogenous cells. CONIDIOGENOUS CELLS enteroblastic, annellidic, doliiform, obclavate, hyaline, smooth. CONIDIA 16–20 × 7–9 µm ($x = 18.2 \times 8.2$ µm, $n = 20$), oblong, straight to slightly curved, rounded at both ends, 4–6-transversely septate, with 1 vertical septum, muriform, smooth, initially pale brown becoming dark brown on maturity.

CULTURE CHARACTERISTICS: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with sparse dense mycelium, off-white to white in the middle, white in the edge, circular, smooth, slightly irregular margin, thin mycelia, radially furrowed, reverse creamy to off-white, flat on the surface.

SPECIMENS EXAMINED: UKRAINE, DONETSK REGION, Donetsk city, Donetsk Botanical Garden, arboretum, on dying twigs and branches of *Robinia pseudoacacia*,

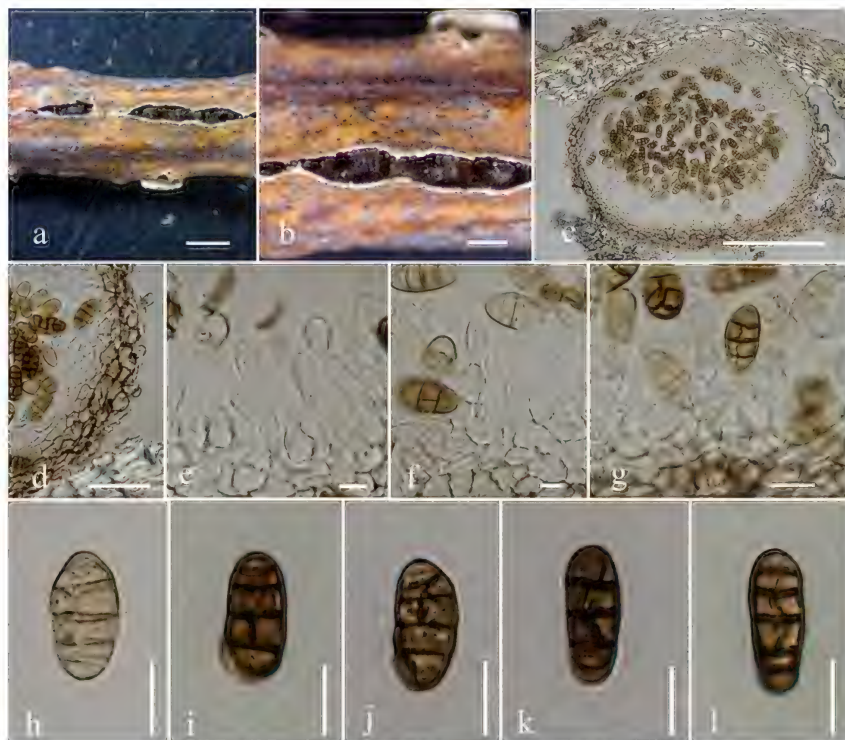


PLATE. 6. *Camarosporidiella robiniicola* (MFLU 17-2469). a, b. Conidiomata on host surface; c. Conidioma, vertical section; d. Peridium; e–g. Conidiogenous cells and developing conidia; h–l. Conidia. Scale bars: a, b = 1000 µm; c = 50 µm; d, h–l = 10 µm; e, f = 5 µm; g = 15 µm.

18 May 2017, Timur S. Bulgakov (MFLU 17-2469; living cultures MFLUCC 18-0775); RUSSIA, ROSTOV REGION, Shakhty city district, Alexandrovsky (Central) Park, trees, on dead twigs of *Robinia pseudoacacia*, 5 November 2017, Timur S. Bulgakov (MFLU 18-0320; living cultures MFLUCC 18-0789; DSM 109791).

NOTES: The isolate MFLUCC 18-0775 clustered with *Camarosporidiella robiniicola* with moderate bootstrap support (ML = 70%, BI = 1). The type species as described by Wijayawardene & al. (2014) differs morphologically from our specimen in its smaller conidiomata (210–240 × 180–220 µm).

HOSTS: *Gleditsia triacanthos*, *Robinia neomexicana* (Wijayawardene & al. 2014, Wanasinghe & al. 2017), *R. pseudoacacia* (this study)

DISTRIBUTION: Italy (Wijayawardene & al. 2014, Wanasinghe & al. 2017), Ukraine and Russia (this study).

Discussion

Morphological circumscription and phylogeny

All phylogenetic analyses show that *Camarosporidiella* is monophyletic as traditionally circumscribed, but not all clades are well supported. Phylogenies derived herein are consistent with those of Wanasinghe & al. (2017), who sampled 99 *Camarosporidiella* strains.

Camarosporidiella moricola (CLADE A) and *C. robiniicola* (CLADE B) isolates cluster in two clades. These two species produce morphologically similar conidia: oblong, ellipsoidal, and pale to dark brown. However, in *C. moricola*, conidiomata appear as small black dots, semi-immersed on the substrate while those of *C. robiniicola* are completely immersed in the substrate. Conidia of *C. robiniicola* are larger ($18\text{--}28 \times 7\text{--}11 \mu\text{m}$) than in *C. moricola* ($8\text{--}15 \times 4\text{--}7.5 \mu\text{m}$) and differ in the number of septa—4–6 transverse septa, 1 vertical septum vs. 1–3 transverse septa, 1–2 vertical septa. ITS and TEF sequences are similar for the two species in this study.

Clade C, which shares a common geographical distribution, comprises *Camarosporidiella clematidis*, *C. elongata*, *C. eufemiana*, *C. laburni*, *C. laburnicola*, *C. mirabellensis*, *C. premilcurensis*, *C. spartii*, and one unidentified isolate (*Camarosporidiella* sp. CPC 12441). Morphological dimensions within this clade overlap for ascomata ($650\text{--}950 \mu\text{m} \times 500\text{--}775 \mu\text{m}$), asci ($130\text{--}255 \mu\text{m} \times 14\text{--}18 \mu\text{m}$), and ascospores ($20\text{--}38 \mu\text{m} \times 8\text{--}12 \mu\text{m}$). However, the species can be distinguished by the number of septa (TABLE 2). There are only <0.5% ITS base pair (bp) differences and <0.8% TEF bp differences separating the species.

Clade D sequences represent two species: *Camarosporidiella celtidis* and *C. populina*. Hyde & al. (2018) separated *C. populina* by its smaller and superficial to semi-immersed conidiomata, phialidic conidiogenous cells, and larger 1–3 transversely septate conidia from *C. celtidis* with larger immersed conidiomata; annellidic integrated conidiogenous cells, and smaller conidia with 2–3 transverse septa and one vertical septum. Nonetheless, only two bp differences separate the *C. populina* and *C. celtidis* ITS sequences. There is no TEF sequence available for *C. populina*. Whether *C. populina* is a separate species warrants further investigation.

Clade E comprises *Camarosporidiella elaeagnicola*. All isolates within the clade are morphologically similar. Our isolate (MFLUCC 18-0782) is morphologically slightly different in having smaller conidiomata and shorter conidia from other species of *C. elaeagnicola* within the clade. But

comparison of ITS and TEF sequences shows no nucleotide bp differences among the species.

Clade F, which comprises the four species *Camarosporidiella caraganicola*, *C. mori*, *C. melnikii*, and *C. italica*, are distinguished by conidiomatal and ascomatal sizes and the morphology of asci, conidia, and ascospores.

Camarosporidiella caraganicola, isolated from dead branches of *Coronilla emerus*, is morphologically similar to *C. italica* in cylindrical asci measuring $150\text{--}190 \times 10\text{--}15 \mu\text{m}$ (Wanasinghe & al. 2017), but differs in its smaller ascospores ($20\text{--}30 \times 7\text{--}10 \mu\text{m}$ vs. $30\text{--}35 \times 12\text{--}14 \mu\text{m}$) and its 3–5 transverse septa, 2–4 vertical septa (vs. 6–8 transverse septa, 2–3 vertical septa in *C. italica*). Within clade F the ITS region of *C. caraganicola* has 10 (1.8%; *C. melnikii*), 3 (0.7%; *C. mori*), and 9 (1.6%; *C. italica*) bp differences, and the TEF region comparison between *C. caraganicola* to that of 5 (0.5%; *C. melnikii*) and 11 (1.2%; *C. italica*) bp differences. No TEF data is available for *C. mori*. *Camarosporidiella mori*, which was isolated from *Morus alba*, shares a conidial size range ($15.5\text{--}21 \times 6.5\text{--}9.5 \mu\text{m}$) with *C. celtidis* and *C. schulzeri*. However, within clade F *C. mori* is phylogenetically distant from *C. celtidis* and *C. schulzeri*, clustering closer to *C. italica*. The *C. mori* ITS sequence shows a 1.7% bp difference to *C. celtidis*, a 1.6% bp difference to *C. schulzeri*, and a 1.3% (7) bp difference to *C. melnikii* and *C. italica*. Although *Camarosporidiella melnikii*, morphologically distinct from *C. caraganicola* and *C. italica*, closely resembles *C. celtidis* in its muriform ascospores measuring $11\text{--}16 \times 5\text{--}6 \mu\text{m}$ with 2–3 transverse septa and without vertical septa, it is phylogenetically separate from *C. celtidis* with 6 (1.1%) ITS and 8 (0.9%) TEF bp differences; *C. melnikii* shows 9 (1.6%) ITS and 11 (1.2%) TEF bp differences from *C. italica*.

The *Camarosporidiella schulzeri* isolates form the monophyletic Clade G (FIG. 1c); *C. schulzeri* resembles *C. elaeagnicola* in its black, immersed $300\text{--}500 \times 300\text{--}550 \mu\text{m}$ conidiomata and similarly sized conidia ($15\text{--}21 \times 8\text{--}12 \mu\text{m}$ vs. $18\text{--}25 \times 9\text{--}13 \mu\text{m}$), both with 2–3 transverse septa and 1 vertical septum. *Camarosporidiella schulzeri* shows 1.06% ITS and 1.12% TEF bp differences to *C. elaeagnicola*, which supports the two species as phylogenetically distinct.

Sequences representing *Camarosporidiella halimodendri*, *C. arezzoensis* and *C. aborescentis*, which form distinct monophyletic groups as clade H, clade I, and clade J, are morphologically similar and phylogenetically close. In addition, there are no bp differences in the ITS and TEF sequences among the three clades.

TABLE 2a. Sexual stage morphology

CLADE	SPECIES	SEXUAL STAGE MORPHOLOGY (µm)				REFERENCE
		ASCOMATA (µm)	ASCI (µm)	ASCOSPORES (µm)	SEPTA (TS ^b , LS ^c)	
A	<i>C. moricola</i>		Undetermined			T
B	<i>C. robiniicola</i>		Undetermined			Wi
C	<i>C. clematidis</i>		Undetermined			Wi
	<i>C. elongata</i>	650–950 × 500–775	140–255 × 14–18	21–38 × 8–12	3–8 TS, 5–7 LS	Wa
	<i>C. eufemiana</i>	350–400 × 450–550	130–150 × 14–15	20–25 × 10–12	3–5 TS, 1 LS	Wa
	<i>C. laburni</i>	400–550 × 500–600	160–190 × 12–16	27–32 × 10–12	6–7 TS, 1–2 LS	Wa
	<i>C. mirabellensis</i>	300–350 × 500–550	140–170 × 12–16	22–27 × 9–11	3–5 TS, 1–2 LS	Wa
	<i>C. premilcurensis</i>	400–450 × 500–600	160–210 × 14–16	22–27 × 10–12	5–7 TS, 1–2 LS	Wa
	<i>C. laburnicola</i>	280–370 × 220–320	125–150 × 9–11	15–21 × 6–8	6–7 TS, 5–6 LS	T
D	<i>C. spartii</i>		Undetermined			Wi
	<i>C. celtidis</i>	200–400 ×300–475	120–160 × 12–15	19.9 × 7.9	3–5 TS, 1–2(–3) LS	Th, Wa
	<i>C. populina</i>		Undetermined			H
E	<i>C. elaeagnicola</i>		Undetermined			Wa
F	<i>C. caraganicola</i>	400–550 × 450–500	150–190 × 10–15	20–30 × 7–10	3–5 TS, 2–4 LS	L
	<i>C. italica</i>	400–450 × 550–600	150–180 × 15–20	30–35 × 12–14		Wa
	<i>C. melnikii</i>		Undetermined			Wa
	<i>C. mori</i>		Undetermined			H
G	<i>C. schulzeri</i>		Undetermined			Wa
H	<i>C. halimodendri</i>		Undetermined			Wa
I	<i>C. arezzoensis</i>	400–500 × 450–550	180–240 × 10–15	19–28 × 9–15	5–7 TS, 4–6 LS	Wa
J	<i>C. aborescentis</i>	350–450 × 500–600	170–210 × 15–18	28–32 × 12–13	5–7 TS, 1–2 LS	L
K	<i>C. mackenziei</i>	500–750 µm diam	131–210 × 15–16	30–35 × 10–12.5	5–6 TS, 1 LS	Wa

^a Reference abbreviations: C = Crous & al. (2018); H = Hyde & al. (2019); L = Liu & al. (2015);
T = Tibpromma & al. (2017); Th = Thambugala & al. (2016); Wa = Wanasinghe & al. (2017);
Wi = Wijayawardene & al. (2014).

^bTS: Transverse septa; ^cLS: Longitudinal septa.

TABLE 2b. Asexual stage morphology

CLADE	SPECIES	ASEXUAL STAGE MORPHOLOGY (μm)				REFERENCE
		CONIDIOMATA (μm)	CONIDIA (μm)	MICROCONIDIA (μm)	SEPTA (TS, LS)	
A	<i>C. moricola</i>	150–340 diam.	8–15 × 4–7.5		1–3 TS, 1–2 VS	T
B	<i>C. robiniicola</i>	180–220 × 210–240	18–28 × 7–11		4–6 TS, 1 VS	Wi
C	<i>C. clematidis</i>	350–380 × 370–425	10–17 × 7–9		2–3 TS, 1 VS	Wi
	<i>C. elongata</i>	400–500 diam.	13–21 × 7–10			Wa
	<i>C. eufemiana</i>		Undetermined			Wa
	<i>C. laburni</i>	300–350 × 300–400	20–30 × 8–11		4–5 TS, 1–2 VS	Wa
	<i>C. laburnicola</i>		Undetermined			T
	<i>C. mirabellensis</i>		Undetermined			Wa
	<i>C. premilcurensis</i>		Undetermined			Wa
D	<i>C. spartii</i>	200–225 × 250–300	13–16 × 6–7		3–4 TS, 2–3 VS	Wi
	<i>C. celtidis</i>	300–350 × 350–450	15–20 × 6–8		2–3 TS, 0 VS	Th, Wa
	<i>C. populina</i>	200–360 diam.	11– 17 × 4–7		1–3 TS, 1 VS	H
E	<i>C. elaeagnicola</i>	300–500 × 300–550	18–25 × 9–13	5–6.5 × 3.5–4.5	2–3 TS, 1 VS	Wa
F	<i>C. caraganicola</i>	413–604 × 280–780	13–26 × 6–13		1–4 TS, 1–4 VS	L
	<i>C. italica</i>		Undetermined			Wa
	<i>C. melnikii</i>	350–550 × 300–500	11–16 × 5–6	7–12 × 4–7	2–3 TS, 0 VS	Wa
	<i>C. mori</i>	370–520 × 220–430	15.5–21 × 6.5–9.5		4 TS, 1 VS	H
G	<i>C. schulzeri</i>	370–420 × 380–460	15–21 × 8–12	4.5–6.5 × 4.5–5.5	2–3 TS, 1 VS	Wa
H	<i>C. halimodendri</i>	500–600 × 350–600	18–25 × 8–12	4.5–7.5 × 3.5–4.5	4–6 TS, 1–2 VS	Wa
I	<i>C. arezzoensis</i>	300–400 × 300–350	20–28 × 6–9	5–7.5 × 3.5–4.5	4–7 TS, 1–2 VS	Wa
J	<i>C. aborescentis</i>	350–600 × 490– 770	12–25 × 5–13		1–3 TS, 1–4 VS	L
K	<i>C. mackenziei</i>	450–550 × 500–600	17–25 × 9–13	6.5–8 × 4–6	3–4 TS, 1–2 VS	Wa

^a Reference abbreviations: see TABLE 2a footnote.

TABLE 2c. Host substrata per clade/species

CLADE	SPECIES	HOSTS
A	<i>C. moricola</i>	<i>Morus alba</i> , <i>M. nigra</i> (Moraceae)
B	<i>C. robinicola</i>	<i>Gleditsia triacanthos</i> , <i>Robinia neomexicana</i> , <i>R. pseudoacacia</i> (Fabaceae)
C	<i>C. clematidis</i>	<i>Clematis vitalba</i> (Ranunculaceae)
	<i>C. elongata</i>	<i>Cytisus scoparius</i> , <i>Robinia pseudoacacia</i> (Fabaceae)
	<i>C. eufemiana</i>	<i>Cytisus</i> sp. (Fabaceae)
	<i>C. laburni</i>	<i>Laburnum anagyroides</i> (Fabaceae)
	<i>C. laburnicola</i>	<i>Laburnum anagyroides</i> (Fabaceae)
	<i>C. mirabellensis</i>	<i>Robinia pseudoacacia</i> (Fabaceae)
	<i>C. premilcurensis</i>	<i>Cytisus</i> sp. (Fabaceae)
	<i>C. spartii</i>	<i>Bassia</i> sp. (Amaranthaceae), <i>Cytisus</i> sp. (Fabaceae)
	<i>C. celtidis</i>	<i>Ailanthus altissima</i> (Simaroubaceae), <i>Betula pendula</i> (Betulaceae), <i>Celtis occidentalis</i> (Cannabaceae), <i>Elymus repens</i> (Poaceae), <i>Gleditsia triacanthos</i> (Fabaceae), <i>Maclura pomifera</i> , <i>Morus alba</i> (Moraceae), <i>Prunus padus</i> , <i>Robinia</i> sp., <i>Spiraea</i> sp (Rosaceae), <i>Ulmus pumila</i> (Ulmaceae).
	<i>C. populina</i>	<i>Populus nigra</i> var. <i>italica</i> (Salicaceae)
E	<i>C. elaeagnicola</i>	<i>Artemisia santonicum</i> (Asteraceae), <i>Cytisus ruthenicus</i> (Fabaceae), <i>Elaeagnus angustifolia</i> (Elaeagnaceae)
F	<i>C. caraganicola</i>	<i>Amorpha fruticosa</i> , <i>Caragana frutex</i> (Fabaceae)
	<i>C. italica</i>	<i>Hippocrepis emerus</i> (Fabaceae)
	<i>C. melnikii</i>	<i>Caragana frutex</i> (Fabaceae)
	<i>C. mori</i>	<i>Morus alba</i> , <i>M. nigra</i> (Moraceae)
G	<i>C. schulzeri</i>	<i>Gleditsia triacanthos</i> , <i>Elaeagnus angustifolia</i> (Fabaceae)
H	<i>C. halimodendri</i>	<i>Caragana frutex</i> , <i>C. halodendron</i> , <i>Cytisus podolicus</i> , <i>Robinia pseudoacacia</i> (Fabaceae), <i>Lycium barbarum</i> (Solanaceae)
I	<i>C. arezzoensis</i>	<i>Amorpha</i> sp., <i>Cytisus</i> sp. (Fabaceae)
J	<i>C. aborescentis</i>	<i>Colutea arborescens</i> , <i>C. orientalis</i> , <i>Cytisus borysthenticus</i> (Fabaceae)
K	<i>C. mackenziei</i>	<i>Caragana arborescens</i> , <i>Caragana</i> sp. (Fabaceae)

Clade K comprises isolates representing *Camarosporidiella mackenziei* and two previously unidentified species. *Camarosporidiella mackenziei* was previously isolated from *Caragana arborescens* from south European Russia. While there are no ITS bp differences separating *C. mackenziei* and *Camarosporidiella* sp. CPC 25960 and CPC 25962, TEF comparisons reveal

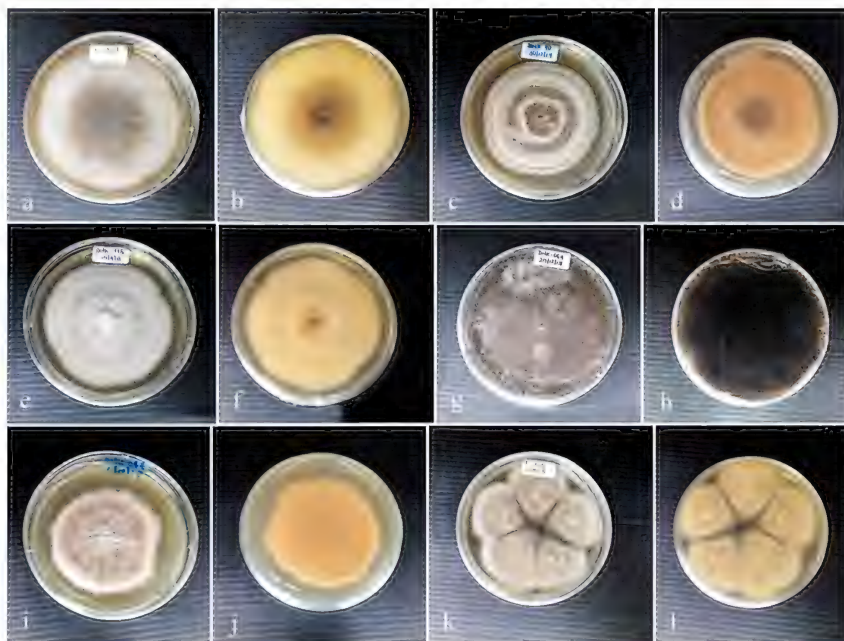


FIG. 2. *Camarosporidiella* spp. cultures. a, b: *C. halimodendri*. c, d: *C. celtidis*. e, f: *C. caraganicola*. g, h: *C. elaeagnicola*. i, j: *C. robiniicola*. k, l: *C. moricola*.

a 0.77% (7) bp difference with CPC 25960 and 0.66% (6 bp) difference with CPC 25962. Recently, Crous & al. (2018), who described the sexual morph of *C. mackenziei*, identified CPC 25960 and CPC 25962 (isolated from *Caragana* sp. in Finland) as *C. mackenziei*.

Identification of *Camarosporidiella* species using ITS region can be challenging, as it does not contain sufficient variation for distinguishing between species, although it is useful in BLAST searches of the NCBI database to get information on species clusters and to confirm new sequences against curated sequences (Doilom & al. 2017). Nonetheless, in this study, ITS-based phylogenies resolved the clades (data not shown) very well, even while pairwise alignment revealed very little difference (<1%) among species. The TEF region, which has been widely used in the taxonomy and systematics of *Camarosporidiella* (Liu & al. 2017, Tibpromma & al. 2017, Wanasinghe & al. 2017), provided better resolution for species-level identification (data

not shown). Yet, bp differences among TEF sequences across species were likewise very small ($< 1\%$). Therefore, using the ITS marker alone to identify *Camarosporidiella* species is probably not sufficient, requiring protein-coding gene sequences as well. A RPB2-based phylogeny might give better results and greater bp differences among species compared to TEF. Further studies are required to see whether amplifying RPB2 gene fragments is possible and useful for identifying *Camarosporidiella* species. If so, we encourage researchers to deposit *Camarosporidiella* RPB2 sequence data in GenBank.

Diversity and host association

Camarosporidiella species are distributed over a wide host range, with higher percentages in *Fabaceae* (45%), *Moraceae* (22%), and *Elaeagnaceae* (12%) (FIG. 3). Most species have been named based on the host from which the fungus was isolated. In the present study, *C. caraganicola*, *C. celtidis* and *C. halimodendri* comprise new host records for Russia. One of our isolates, MFLUCC 18-0786,

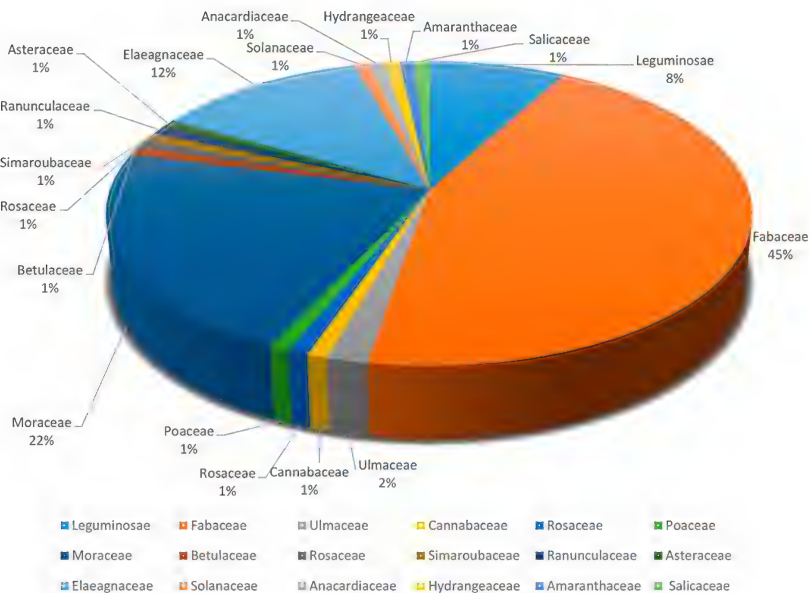


FIG 3. Family affiliations of hosts of *Camarosporidiella* strains with molecular data.

clustered in Clade F (FIG. 1) among *Camarosporidiella caraganicola* sequences. We add a new host to the fungal records from *Fabaceae* as *C. caraganicola* has not been previously reported on *Amorpha fruticosa*. The morphology of *C. caraganicola* MFLUCC 18-0786 fully agree with the descriptions provided by Liu & al. (2015) and Wanasinghe & al. (2017).

Camarosporidiella celtidis, previously described as *Cucurbitaria celtidis* by Shear (1902), was previously isolated from *Celtis occidentalis* in Osborne, Kansas. The species was transferred to *Camarosporium* by Thambugala & al. (2016) based on molecular data from a fresh collection. *Cucurbitaria celtidis* was later re-circumscribed as *Camarosporidiella celtidis* by Wanasinghe & al. (2017), who illustrated its asexual morph. *Camarosporidiella celtidis* has been reported on a wide range of hosts including *Celtis occidentalis* (*Cannabaceae*), *Gleditsia triacanthos* (*Fabaceae*), *Maclura pomifera* (*Moraceae*), *Spiraea* sp. (*Rosaceae*), *Prunus padus* (*Rosaceae*), *Morus alba* (*Moraceae*), *Elymus repens* (*Poaceae*), *Betula pendula* (*Betulaceae*), and *Ailanthus altissima* (*Simaroubaceae*) (Ellis & Everhart 1894, Shear 1902, Thambugala & al. 2016, Wanasinghe & al. 2017). In the present study, *C. celtidis* was recovered from dead *Ulmus pumila* twigs in Ukraine. Our new isolate also matches the descriptions of Wanasinghe & al. (2017).

Likewise, *Camarosporidiella halimodendri* has been collected in Iran by Farr & Rossman (2017). The isolate *C. halimodendri* (MFLUCC 18-0767) from *Robinia pseudoacacia* clustered in Clade H with other *C. halimodendri* isolates. We found no description for *C. halimodendri* isolates from *Robinia pseudoacacia* in any scientific publication. From previous studies, we know that phenotypic variation often depends on host substrata, environmental conditions, and geographical location (Jain & Fries 2009, Hewitt & al. 2016, Elliot & al. 2018, De Silva & al. 2016, Promputtha & al. 2019). We should note that MFLUCC 18-0767 morphologically differs slightly from the other *C. halimodendri* in this clade in its shorter conidia and different microconidia.

Camarosporidiella elaeagnicola has been collected on *Elaeagnus angustifolia* from Russia and from *E. rhamnoides* in Germany. We regard our three isolates grouped in Clade E as representing additional collections of *C. elaeagnicola*. *Camarosporidiella*

robiniicola, previously collected from *Robinia pseudoacacia* in Italy, was first described by Wijayawardene & al. (2014), and later Wanasinghe & al. (2017) reported additional collections by adding seven new *C. robiniicola* strains; here we present our two isolates in Clade B as representing new collections of *C. robiniicola* from Russia. *Camarosporidiella moricola* was originally proposed in Tibpromma & al. (2017; as *Camarosporium moricola*), and Wanasinghe & al. (2017) added twelve strains collected from *Morus alba* in Russia. We identify our six strains MFLUCC 18-0766, MFLUCC 18-0768, MFLUCC 18-0769, MFLUCC 18-0770, MFLUCC 18-0771, and MFLUCC 18-0772 (also from Russia) and MFLU 17-0991 (a new record from Italy on *Morus nigra*) as *C. moricola* based on cultural and morphological characteristics.

Our current data indicate greater species diversity and a much wider range of habitat for *Camarosporidiella* species in many countries of the northern hemisphere. It is very likely that many *Camarosporidiellaceae* were initially described as species in *Camarosporium* s. lat., as other anamorphic fungi with pigmented septate conidia (e.g., *Dichomera*, *Hendersonia*), or their sexual stages as ascomycetes with pigmented septate ascospores (e.g., *Cucurbitaria*, *Pleospora*). For example, 78 *Camarosporium* spp., 3 *Dichomera* spp., 54 *Hendersonia* spp., and 48 *Cucurbitaria* spp. were previously recorded on Ukraine territory alone (Andrianova & al. 2006), many of which on the same host plant species now cited for *Camarosporidiella* species collected in the adjacent Rostov region of Russia. Undoubtedly at least some of those fungi and *Camarosporidiella* species are conspecific. Unfortunately, the original species descriptions of most species in *Camarosporium*, *Dichomera*, and *Hendersonia* are very brief, incomplete, and sometimes even controversial. Therefore, it is difficult to compare species described in the 21st century with 19th and 20th century descriptions based solely on morphological features.

Camarosporidiella species are mainly saprobic on dead twigs and branches of woody plants, with some being necrotrophic pathogens causing necroses of twigs and branches of woody angiosperms. This implies a rather wide host specialization for the pathogenic species. Although most *Camarosporidiella* species were named based on the host plant from which they were isolated for the first time, it is

already clear that many species (especially saprobic) can potentially grow on angiosperms of many genera, families, orders, and classes. Nevertheless, our observations indicate that each *Camarosporidiella* species usually colonizes plants of a certain plant genus or plant family, although many species may colonize closely related (or even not so closely related) woody plants. Occasionally different *Camarosporidiella* species coexist on the same plant species, often simultaneously on the same plant.

For example, *Camarosporidiella caraganicola*, *C. halimodendri*, and *C. melnikii* were all found on *Caragana frutex*; *C. robiniicola* and *C. schulzeri* were both found on *Gleditsia triacanthos*; and *Camarosporidiella mirabellensis*, *C. robiniicola*, and *C. schulzeri* were found on *Robinia pseudoacacia* in Russia and Italy (Wanasinghe & al. 2017). *Camarosporidiella robiniicola* was found not only on its primary hosts (*Robinia pseudoacacia* and other *Robinia* spp.), but also on another closely related leguminous tree—*Gleditsia triacanthos* (Wanasinghe & al. 2017) as well as an unrelated introduced shrub *Cotinus coggygria* Scop. (Liu & al. 2015) growing under *Robinia pseudoacacia*. In this study, we found *Camarosporidiella caraganicola* on an *Amorpha fruticosa* surrounded by *Caragana frutex* shrubs. *Camarosporidiella elaeagnicola* was found not only on its main host plant (*Elaeagnus angustifolia*), but also on the aboriginal dwarf semi-shrub *Artemisia santonica* (Wanasinghe & al. 2017), aboriginal low shrub *Cytisus ruthenicus*, and introduced *Robinia pseudoacacia* (this study); but in all cases those new host plants were located close to *Elaeagnus angustifolia* trees affected by *Camarosporidiella elaeagnicola*.

We hypothesize that many necrotrophic *Camarosporidiella* species move from main host plants to nearest closely related and even distantly related plants, especially when growing together in botanical gardens, arboreta, artificial forests, urban parks, and private gardens. Saprobiic *Camarosporidiella* species therefore can grow on very wide range of host plants. For example, saprobic *C. celtidis* was found on many plants of many families, so we could expect the species to be found on dead stems, twigs, and branches of many other plant species. It is likely that *C. celtidis* was first recorded as *Hendersonia sarmentorum* Westend. or some other *Hendersonia* species in Ukraine (Andrianova & al. 2006).

It is notable that the hosts of many *Camarosporidiella* species originate in North America (*Amorpha fruticosa*, *Celtis occidentalis*, *Gleditsia triacanthos*, *Robinia pseudoacacia*, *R. neomexicana*), Central Asia (*Caragana halodendron*, *Elaeagnus angustifolia*, *Morus nigra*), and East Asia (*Ailanthus altissima*, *Caragana arborescens*, *Cotinus coggygria*, *Lycium barbarum*, *Morus alba*). These plants were introduced to many European countries (including Italy and Russia) over a century ago, and today many have become invasive in some regions of Russia (The Black Data Book of the flora of Central Russia 2009) and Europe (DAISIE 2009). Because of their obligate associations with alien plants, many *Camarosporidiella* species might also be treated as alien fungal species in territories where they are found for the first time.

Many *Camarosporidiella* species were both weakly supported in our phylogenetic analyses and morphologically similar. We also cannot rely on cultural variation or on morphological descriptions of specimens collected in the 19th–20th centuries to delimit species. *Camarosporidiella* is a complex taxonomic group requiring integrative taxonomy rather than phylogenies based only on neutral markers (Zamora & al. 2015, Caparrós & al. 2016, Hyde & al. 2020, Jayasiri & al. 2017, Konta & al. 2020, Sharma & al. 2016). For these reasons, new specimen collections and further research on *Camarosporidiella* in Europe, Central and East Asia, and North America are needed to clarify the origins of many species, their natural diversity, and relationships.

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